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THE SPECIFIC GRAVITY OF SOME FRESH-WATER ANIMALS IN RELATION TO THEIR HABITS, DEVELOPMENT, AND COMPOSITION.[1]

STEPHEN R. WILLIAMS.

THE questions I have examined are: What is the specific gravity of animals living in water, and what bearing does their specific gravity have on their life histories?

These questions suggest the underlying problem of the specific gravity of protoplasms. I say protoplasms because two eggs, though very similar in appearance, existing under exactly the same conditions, may develop into two widely different animals.

The first part of my paper deals with the specific gravities of adult animals. The second part is a description of a number of series of growing tadpoles, in which I have ascertained, besides their specific gravity, their dry weight, and thus the percentage of water they contain. The third section of the paper has reference to the location of the water which, as shown by Davenport (**'97–99**, p. 285), is imbibed by the tadpole in its period of rapid growth.

I.

Protoplasm with its structure and functions very little specialized will be best found in simple, free-swimming water animals. An Amœba is apparently a body of simple protoplasm, and if a method delicate enough to find its specific gravity were devised, we should know very exactly how amœbic protoplasm compares in weight with its own volume of pure water, and how much effort would be necessary on the part of the Amœba to maintain itself at a given level. I have, however, not been able to get the specific gravity of Amœbæ. But the larger soft-bodied animals, or animals with their shells removed, those with a small amount of foreign matter only, and especially embryos, offer favorable fields for the study of the specific gravity of protoplasms, and consequently I have made use of them.

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[1] *Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy at Harvard College.* E. L. Mark, Director. No. 107.

Any information concerning the specific gravity of organisms will be of use in explaining motions, positions, and possible foods of the different animals. Tadpoles, found to be negatively geotactic by Miss Platt ('99), are forced to swim or to adhere by their suckers if they wish to remain above the bottom. The attitude of young tadpoles in an aquarium, as they hang tail downwards while clinging to the glass sides by their suckers, is due to the pull of gravity. Outdoors very few young tadpoles are seen at the surface of ponds where one knows they abound, though older stages are common at the surface. Stir up the bottom, and the surface for an instant will be black with tadpoles clinging to the bottom débris. An individual of a later stage whose intestine is filled with gas floats, can no longer feed on the bottom algæ, and is outstripped in growth by his normal fellows.

In determining specific gravity I have used the method suggested by Davenport ('97–99) and used by Miss Platt ('99), that of placing the animal in a solution of its own density. The density of this solution can be varied at will by the addition of known amounts of the dissolved substance or of water.

I found it necessary to stupefy all the free-swimming animals experimented upon. For this purpose I generally used chloroform as the most convenient reagent. It is, however, unsatisfactory for Planaria, as the irritation causes a slime to be secreted, which buoys up the animal greatly. It causes Protozoa to burst. For Planarians a solution of CO_2 gas in water is excellent. For Stentors and Bursaria, being unable to stupefy without killing, I tried four per cent formol, absolute alcohol, CO_2, and chloroform, each without success. One-half per cent osmic acid and hot Perenyi's solution were fairly good, though most of the Stentors contracted to balls under the influence of the reagents. Flemming's solution (weak) gave the best results. Many Stentors kept their extended shape and upon microscopic inspection appeared little altered.

I used gum arabic to regulate the density of my solutions, since, as suggested by Dr. Davenport, it is not injurious to animals immersed in it. It is more convenient to take a solution of high specific gravity and lower this gradually by adding water, than to increase the density by adding known weights of gum. Since different pieces of gum vary noticeably in density, two solutions made in exactly the same proportions may vary perceptibly in their buoyant effect. Consequently, to get a consistently acting medium which can be used throughout a series of experiments and which, each time it is made up, acts in about the same way, I made up a stock solution of 15 grams gum arabic and 30 cc. of distilled water. With a bit of camphor to keep out bacteria and a glass-stoppered vessel to prevent evaporation, there is no appreciable change in a month's time. A long pipette and a large test-tube, both marked in cubic centimeters on the outside, are the only apparatus necessary. The marking on the outside of the test-tube is absolutely essential to avoid uncertainty as to how many cubic centimeters have been added to the mixture.

In making a series of gum-arabic solutions I found that a gram of gum arabic when dissolved occupies between 0.66 and 0.72 cc. According to Landolt und Börnstein's Tabellen ('**94**), the specific gravity of the gums which are included under the name "gum arabic" varies between 1.31 and 1.45. The space that one gram occupies varies, then, between 0.763 and 0.689 cc. Comparing this with the observed volumes, I feel justified in assuming as an average the space value 0.7 cc. for one gram of dissolved gum arabic. On this basis the two tables which follow (p. 98) have been computed.

To make my stock solution I used 15 grams gum, which at 0.7 cc. space per gram occupies 10.5 cc. Adding 30 cc. of (distilled) water, the whole volume is 40.5 cc. The total weight is 45 grams, and weight divided by volume gives 1.111 + as the specific gravity of the mixture. The second number in the table is found by adding to 1 cc. of this mixture 1 cc. of pure water and dividing the combined weight (2.111+) by the combined volume (2), which gives 1.056 —. For the third place in the table I added to 1 cc. of the original mixture 2 cc. of pure water, 3.111 + divided by 3 giving 1.037, and so on.

TABLE I. — SPECIFIC GRAVITY OF SUCCESSIVE DILUTIONS OF GUM-ARABIC SOLUTION.

Starting with 1 cc. of the stock solution and adding water 1 cc. at a time, 1 gram gum arabic being reckoned as the equivalent of 0.7 cc. volume.

Vol. added	0	1	2	3	4	5	6	7	8	9
Sp. gr.	1.111+	1.056−	1.037	1.028	1.022	1.0185	1.016	1.014	1.012	1.011
Vol. added	10	11	12	13	14	15	16	17	18	19
Sp. gr.	1.010	1.009	1.0085	1.008	1.0074	1.007	1.0065	1.006	1.0058	1.0055
Vol. added	20	21	22	23	24	25	26	27	28	29
Sp. gr.	1.0053	1.005	1.0048	1.0046	1.0044	1.0042	1.0041	1.004	1.0038	1.0037
Vol. added	30	31	32	33	34	35	36	37	38	39
Sp. gr.	1.0036	1.0034	1.0033	1.0032	1.0031	1.003	1.003	1.003	1.0029	1.0028

TABLE II. — MODIFICATION FOR USE WITH MINUTE ANIMALS.

By starting with $\frac{1}{4}$ cc. of the stock solution and adding $\frac{1}{12}$ cc. of water at a time, there is a smaller interval between two steps than is possible by the method of Table I.

Vol. added	0	.33	.67	1	1.33	1.67	2	2.33	2.67	3
Sp. gr.	1.111	1.083	1.0667	1.056	1.047	1.041	1.037	1.033	1.030	1.028
Vol. added	3.33	3.67	4	4.33	4.67	5	5.33	5.67	6	6.33
Sp. gr.	1.025	1.024	1.022	1.021−	1.019+	1.018+	1.017	1.0165	1.016−	1.015
Vol. added	6.67	7	7.33							
Sp. gr.	1.0145	1.014	1.013							

I experimented with a Beaumé's hydrometer to test how nearly the calculated values of my table matched the observed values of the hydrometer reading. One experiment began with water giving a hydrometer reading of 1.003. After dissolving 5 grams of gum in 240 cc. of this water, the hydrometer reading was 1.011. Deducting the discrepancy of the reading for the water taken, the true specific gravity of the solution was 1.008. (The exact reading is difficult to be certain of, because of capillarity. I took the mean of a number of readings made by myself and by other persons reading independently.) By dividing the volume, 243.5 (counting one gram space as 0.7 cc., as in the tables), into the weight, 245, the specific gravity resulting is 1.006 +. So the hydrometer read nearly 0.02 higher than the calculated specific gravity. In another test, to 238 cc. distilled water at slightly more than 1.000 sp. gr., 5 grams of gum were added, whereupon the hydrometer stood at 1.010. The calculated gravity is 1.0062+, a little less than 0.004 lower than the hydrometer reading. My results, then, are somewhat lower than the hydrometer would have made them. Taking into account the possible variation in the specific gravity of the gum, the two correspond quite closely.

To determine whether different parts of a gum solution were of the same density, I tested a single mixture: 254 cc. of a solution in which the hydrometer stood at 1.037 were divided into upper and lower halves as gently as possible. To each half was then added its own volume of pure water. Testing each, it was found that the lower half had a specific gravity of 1.020, while the upper read 1.018. As the solution had stood for some hours before being divided, I have assumed that the upper and lower halves of a solution were of the same density.

I have written above each sp. gr. value in the table the fraction of the starting amount (in case of Table II $\frac{1}{4}$ cc. of the gum-arabic mixture) which was added in the form of pure water. Taking, for example, the sixth place in Table II, the starting quantity of the mixture + 1.67 times its volume of water has a resulting specific gravity of 1.041.

In performing an experiment I put 1 cc. of the gum mixture into a test-tube with a long pipette, taking care not to draw the gum above the 1 cc. mark and not to get any on the sides of the test-tube. Then I lifted the animals with as little water as possible into the solution. Where I knew that the specific gravity was less than 1.111, I took 1 cc. of water with them. Animals must be placed underneath the surface of the liquid, not dropped upon it, as some are buoyed up by the surface film, and so do not sink in solutions lighter than themselves. (Planaria and snails are thus supported in common pond water.) As it is very difficult to force out the gum adhering to the sides of the pipette, I made an allowance for the diminution of bore due to the adhering gum when adding the first cubic centimeter of pure water. By using this pipette to add the water, the gum mixture will soon be washed completely out into the test-tube, where it belongs.

The very heavy bodies — such as the eggs — and the very light ones — such as the older tadpoles (in general, the ends of the series) — afford the least accurate determinations of their specific gravity. To have a uniform standard for all, I assumed that in each case, after the addition of more water, an animal floated unless in sinking it touched the bottom or curving end of the test-tube.

I give my results in the form of a table (in which the animals are arranged according to their systematic relations) showing the number of specimens used, the average specific gravity, and the probable error. In the case of starred animals the solutions given by Table II were employed. This involved less rough treatment than by using the method of Table I.

There are five animals at the end of the table which were not tested in sufficient numbers to warrant comparison with the others.

All the free-swimming animals tested (excepting old tadpoles) tend, when quiescent, to be at the bottom and to rise must swim. That the lighter animals need less effort to swim is well illustrated by the two entomostracans, Cypridopsis and Simocephalus. Simocephalus moves without much effort and often very slowly in the water. Cypridopsis, on the other hand, must move rapidly and continuously or it sinks. It requires a distinct effort for a mosquito larva to get to the surface.

TABLE III.

ANIMAL.	NUMBER OF SPECIMENS.	AVERAGE SP. GR.	PROBABLE ERROR.
*Stentor cœruleus Ehrbg.	72	1.016+	.0016
*Bursaria (*sp.*?)	66	1.0142	.00067
Hydra viridis L.	18	1.0095	.0013
Hydra { fusca L. or grisea L. }	6	1.0115	.0009
Cordylophora lacustris Allm.	5 heads	1.016	—
Planaria maculata Leidy	27	1.030	.0026
*Rotifer vulgaris Ehrbg.	15	1.021	—
Dero intermedia Cragin	36	1.022	.002
Cyclops albidus Jurine	16	1.0222	.0029
Simocephalus vetula Müller	17	1.0136	.0012
Cypridopsis vidua Müller	40	1.046	—
Culex (larvæ)	11	1.0185	.0002
Agrion larvæ	8	1.046	—
Aquatic fly larvæ (*sp.*?)	Many	1.0185	—
Physa (shell removed)	4	1.037	—
Nephelis (*sp.*?)	1	1.037	—
Asellus	3	1.037	—

When there, the surface film holds up the breathing tube with its spreading hairs. Whenever that support is lost the animal sinks. A Cyclops, when moving slowly, can be seen to move upwards with a jerking motion, then to sink slightly, then to jerk again, and so on. To remain motionless it must have its antennæ on the surface film.

A sinking animal, like a lifeless body, always falls with the heavy end downward. Many animals do not give special evidence in this direction. Cyclops usually sinks head downward, the tail being at an angle of 45° with the horizon. Hydra, unless unusually dense near the mouth (for instance, with food in the gastrovascular cavity), sinks foot downward. One with a bud sank bud downward.

In the tadpole the center of gravity changes position in the course of development. Up to a length of about 6 mm., it is in the head region, for that always sinks first. In later stages the center of gravity moves backward nearly to the root of the tail, and tadpoles hang in the water with the tail at least 20° lower than the head. Many of the older ones seem no heavier than water. As soon as tadpoles begin to depend on food taken into the alimentary canal from without, the canal may become filled with air or gas, so that the animal floats belly up. This condition is not permanent, for I have isolated such floating tadpoles and they regained the bottom in the course of a day. I have seen a tadpole force from its mouth as many as twelve bubbles of gas. After attaining the length of 10–11 mm., the specific gravity of the tadpole depends much on the condition of the animal and on the development of the lungs. The refuse of the food in the alimentary canal, which consists of partially digested green water plants and many diatoms, may aid the animal in sinking. It certainly helps move back the center of gravity of the animal from the head region toward the tail.

II.

I have found the specific gravity of four series of tadpoles — two in the spring of 1898 and two in the spring of 1899. In each instance one series was the young of *Rana silvatica*, the other those of *Bufo lentiginosus*.

TABLE IV. — SPECIFIC GRAVITY OF FROG AND TOAD TADPOLES.

LENGTH IN MM. =	ROUND EGGS.	2–3	4–5	6–7	8–9	10–11	12–13	14–15	16–16+
Rana silvatica, 1898	—	—	1.022	1.013	—	1.013	1.008	1.005	1.0055
Rana silvatica, 1899	—	1.111	1.11–	1.050	1.042	1.028	—	1.010	1.0052
Bufo lentiginosus, 1898	1.038	1.037	1.037	—	1.022	1.013	1.013	1.010	—
Bufo lentiginosus, 1899	1.037	1.037	1.030	1.022	1.017	—	1.016	1.016	—

This table calls for a few remarks.

I have been able to get no good determinations of the specific gravity of the eggs of the frog, for unless the egg envelope is removed, the specific gravity is too high; and if the envelope is removed from the youngest eggs, they break badly in the solution. The toads for the two years correspond fairly well with each other, but the drop in specific gravity began a little earlier in their growth in 1899 than in 1898. There is a great difference in the two series of frog tadpoles, however, that of 1898 being much lighter. Even allowing for possible individual variation, the discrepancy is still too great to be accounted for by the faults of the method.

In looking back at the history of the two cases I find an explanation, which is based upon the work of Galloway ('**98**), who found experimentally that tadpoles of Rana, Amblystoma, and Bufo, kept in a warm place, imbibed proportionately more water in reaching a certain stage than did those kept in the cold. My first series of observations (Table IV) was made on eggs of *Rana silvatica*, which were obtained in cleavage stages March 26, 1898. These were kept *at room temperature* and hatched out March 28–31 (two to five days), some reaching the length of 7 mm. by the latter date. The second series was collected April 11, 1899, and kept *out of doors* in a shallow basin on the ledge of a north window. On April 22 they had reached a length of 7 mm. (after a period of eleven days), although still in the egg, and on that day I brought them into the room to hasten their hatching. Since the specific gravity of the embryos in the second series was throughout so much greater than that of the first, I infer that they must have contained much less water, therefore have had smaller lymph spaces and smaller vacuolated cell regions and water spaces. That is, the embryos reared in a higher temperature must have imbibed more water than those exposed to the lower temperature.

But while the specific gravity depends on the amount of water absorbed by the tissues of the embryo, it also depends on the amount of animal matter. The proportional amount of this animal matter present has been ascertained by weighing, desiccating, weighing again, and computing what per cent of the first weight the dry weight is. Since the animals from one mass of eggs vary individually, I selected them on the basis of length, not age, each observation being based on five or ten individuals of a given length.

In the series of tadpoles of frog and toad I have found the specific gravity, the average fresh weight, the average dry weight, and the percentage dry weight. They were dried in a partial vacuum over sulphuric acid.

Table V. — Rana silvatica.

Date.	Number of Tadpoles.	Length. (mm.)	Average Fresh Weight.	Average Dry Weight	Per Cent Dry Weight.	Specific Gravity.
April 13	5	2½	.00328	.00136	41.4	1.11 +
April 13	5	4	.00344	.00132	38.37	1.11 –
April 21	5	6	.00402	.00142	34.8	1.055
April 22 25	10	7	.00448	.00126	28.1	1.055–1.037
April 18 27	10	8–9	.00540	.00105	19.4	1.037–1.022
April 21	5	9	.00592	.00110	18.58	—
April 21	10	10–11	.00794	.00110	13.9	1.022–1.018
April 22	5	13–14	.02730	.00144	5.25	1.010
April 26	5	16–17	.04100	.00208	5	—
April 28	5	16	.05090	.00230	4.5	1.009–1.0065
May 1	5	20	.06750	.00356	5.2	1.007

Table VI. — Bufo lentiginosus.

Date.	Number of Tadpoles.	Length. (mm.)	Average Fresh Weight.	Average Dry Weight.	Per Cent Dry Weight.	Specific Gravity.
May 1	10	3–4	.00115	.0005	44.3	1.037
May 1	10	4–5	.00217	.0007	32.2	1.037
May 2	10	6	.00339	.00065	19.1	1.025
May 3	10	7	.00354	.00062	17.5	1.022
May 10	10	8–10	.00867	.00077	8.8	1.018–1.016
May 10	10	10	.01477	.00122	8.2	1.016
May 10	10	12	.02496	.00196	7.8	1.018–1.016
May 11	10	13–15	.04455	.00327	7.3	—

These tables show:

1. That the animals, while continually increasing in total weight, really decrease in dry weight up to the age (about 10 mm. long in the frogs) where they take in food from without.

2. That the specific gravity decreases with the increase in volume, as one would expect if the increased volume is due to imbibition of water.

3. That the percentage of dry weight continues to decrease even after the absolute dry weight, owing to the acquisition of food from without, begins to increase. A similar set of results expressed in the form of a curve is given by Davenport ('**97–99**, p. 285).

In the case of the toad series growth was so slow that for the greater lengths (8 mm. and upwards) I took toads from out of doors. All had reached the feeding stage, the intestines of all being full, and since the conditions were the same and the lengths not greatly different, their specific gravities were essentially the same.

The preceding table was based on developing forms of Amphibians. I give also for comparison the relation which exists between dry weight and total weight in a few individuals of essentially adult fish.

TABLE VII.

	NUMBER OF INDIVIDUALS.	LENGTH. (mm.)	LIVE WEIGHT.	DRY WEIGHT.	PER CENT DRY WEIGHT.
Fundulus . .	2	32	.2090	.0454	21.7
Fundulus . .	1	35	.2780	.0622	22.6
Fundulus . .	2	44	.6336	.1490	23.6
Gasterosteus .	1	30	.1449	.0358	23.4
Gasterosteus .	1	60	1.4041	.3179	28.6

These fish were dried ten days. The larger the fish is, the greater the per cent of dry weight.

As one would expect, the armored stickleback has a greater per cent dry weight than Fundulus.

III.

The last section of the paper has reference to the location of the imbibed water in the tissues of the tadpole. I give three cross-sections from tadpoles of *Rana silvatica* at different ages. They are in black and white, all solid cell tissue being printed black. They are all outlined with the camera to a magnification of 30 diameters.

As nearly as possible they are from corresponding regions of the body — the region just back of the thickened auditory epithelium. No. 1 is taken from a specimen 2½ mm. long.

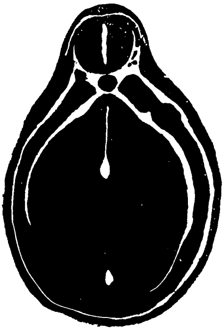

FIG. 1. — Cross-section *R. silvatica*, 2½ mm. long, magnified 30 diam.; tissue black, spaces white.

Plainly there are here very few spaces which may contain water or lymph. The cells also are very crowded and show no vacuolation.

No. 2 is from a 10 mm. tadpole. The change is remarkable, especially in the development of the highly vacuolated mesenchyme. The neural canal is larger, while the cross-section of nervous tissue is not greatly increased.

The cavities of the œsophagus, intestine, and liver are large, and the pronephric tubules also increase the interior space.

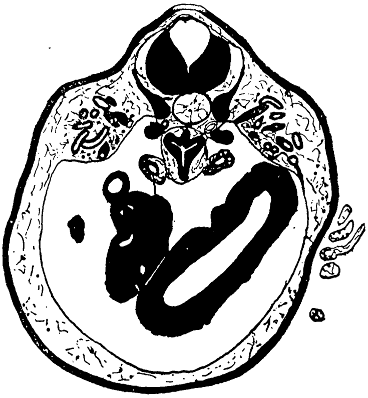

FIG. 2. — Cross-section *R. silvatica*, 10 mm. long, magnified 30 diam.

As the best example of the change in individual cells, I call attention to those of the chorda, which are very strongly vacuolated.

The cross-section (Fig. 3) from a 20 mm. tadpole shows that, except for the cluster of cells on the right which forms the limb bud, the area of solid tissue has decreased greatly. The epidermis is very thin compared to either of the other examples, and the œsophagus and intestinal wall are not more than half as thick as in the preceding stage.

Table V shows that the actual tissue (dry weight) in specimen No. 2 must have been less than in No. 1. That the actual

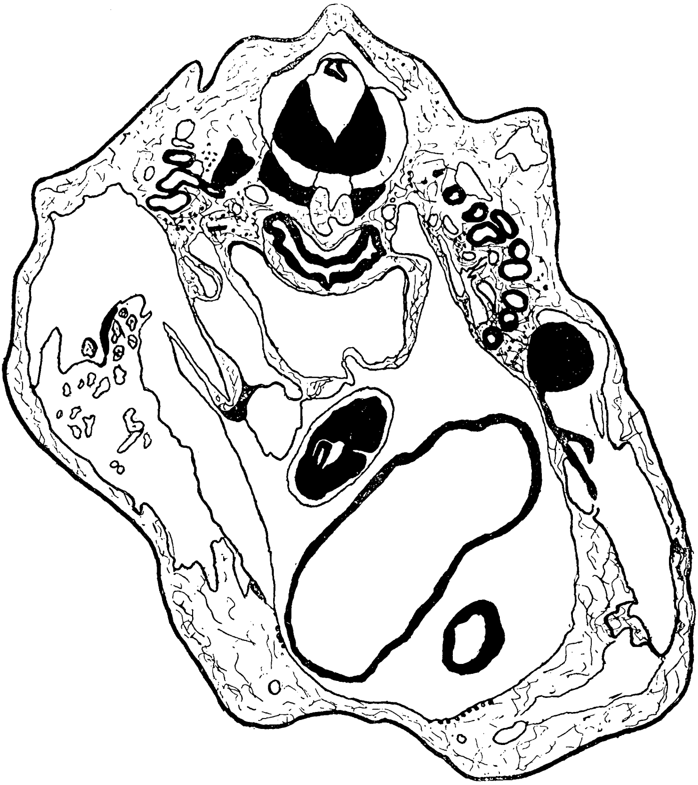

FIG. 3. — Cross-section *R. silvatica*, 20 mm. long, magnified 30 diam.

tissue is greater in the 20 mm. tadpole is due to the fact that the tadpole has been taking in solid food for ten days.

RESULTS.

The specific gravity of certain fresh-water animals was determined and found to vary from 1.0095 (*Hydra viridis*) to a maximum of 1.0460 (Cypridopsis).

The movements of an animal are closely related to its density, and there is also a correlation between density and food habits.

Of the animals tested, Stentor may represent a typical case of specific gravity in little modified protoplasm. The heavier animals certainly have some specialized tissues which are denser, while in the case of Hydra, the lightest, the extreme vacuolation of the inner layer may well indicate a less representative character of the protoplasm.

In the case of the developing animal the chief tissue to absorb water, and, therefore, the tissue of most rapid increase in bulk, is the mesenchyme. All of the walls of the internal organs, however, grow thinner and less dense as the animal increases in size.

This work has been carried on under Dr. Charles B. Davenport, whose suggestions are the basis of anything of value it may contain.

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